ON THE ANATOMY OF *NATALINA CAFFRA*, FÉR., WITH SPECIAL REFERENCE TO THE STRUCTURE OF THE BUCCAL MASS.

By M. F. WOODWARD, Demonstrator of Zoology, Royal College of Science, London.

Read April 19th, 1895.

PLATE XVII.

SOME years ago, Mr. B. B. Woodward placed at my disposal two live specimens of *N. Caffra* from Port Elizabeth, which he had received through the kindness of Mr. Ponsonby. These were kept alive for some months by supplying them with living specimens of *Helix aspersa* and *H. pomatia*, of which they ate several, and consequently grew considerably in size, one of them adding about half an inch to its shell in three months.

A description of the habits and external characters was given by Mr. B. B. Woodward at a meeting of the Zoological Society.[1]

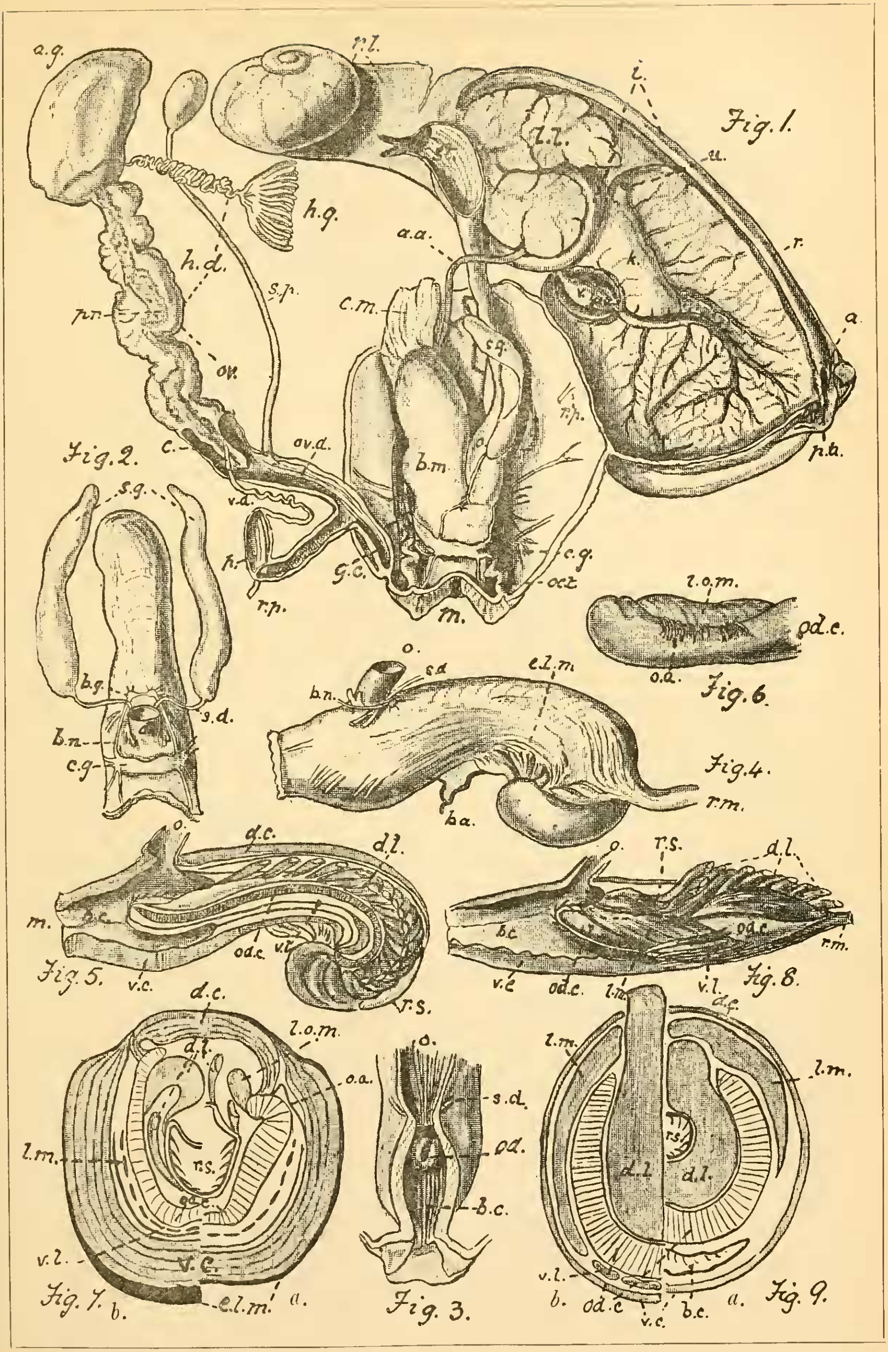
The animals were subsequently killed in an extended condition, and I further made dissections and numerous drawings of the latter. I did not, however, publish any account of their anatomy, as I understood that specimens had been forwarded to Mr. Pilsbry for that purpose, and thought it unnecessary to duplicate his description. Unfortunately, during the voyage to America the animals died, and when received were so much decomposed that Pilsbry was only able to give a very slight account of their anatomy.[2]

Pilsbry[3] has also described the anatomy of *N. Knysnaënsis* from a contracted spirit specimen, and recently Pace has published a short account of the anatomy of *N. Trimeni* in the Proceedings of this Society.[4] Most of these accounts, however, are based on imperfect or badly-contracted spirit specimens, so that it seems advisable to give a more detailed description of the anatomy of this interesting genus founded upon dissections of fresh and carefully-killed specimens.

Natalina Caffra was originally described as *Helix Caffra* by Férussac: it was placed by Albers with the Helices on purely conchological grounds, but in a distinct genus, *Ærope*; this name, being pre-occupied for an Echinoderm, must be dropped, and *Natalina* substituted. The animal was first described by Mörch,[5] who pointed out its true affinities with the Agnatha, from the study of its lingual apparatus.

---

[1] Proc. Zool. Soc. 1889, p. 327.
[2] Proc. Acad. Nat. Sci. Philad. 1890, pp. 241–243.
[3] *Ibid.* 1889, pp. 277–279.
[4] Proc. Malac. Soc. Lond., vol. i, 1895, pp. 232, 233.
[5] Journ. d. Conchyliologie, 1865, p. 395.



M. F. Woodward: del.

ANATOMY OF *NATALINA CAFFRA*, Etc.

Gibbons, in 1880,[1] described the external characters very fully, and I have nothing much to add to his description, except to note the absence of a tail-pore, and the fact that the swollen mantle-border is of a rich orange-colour. As he pointed out, the accessory labial tentacles are very prominent, but I should rather describe them as hatchet-shaped, and note that they appear to be extremely sensitive, being in all probability tactile in function, but not, I think, used for prehension, as suggested for the same tentacles in *Glandina.*

Natalina Caffra, from life.

Gibbons's specimen was fed on boiled potato, but showed a partiality for animal food by seizing a small living *Ennea.* I never observed any tendency on the part of my animals towards a vegetarian diet, but found them to be entirely carnivorous, eating either live snails or raw beefsteak, on which diet they flourished extremely well, the animals growing so large that they rarely withdrew completely into their shells.

Alimentary canal.—The most noticeable anatomical features, which characterize the Agnathous Pulmonates, are the absence of any jaw or beak-like structure, and the enormous size of the buccal mass, the latter structure probably attaining its maximum development in the genus *Natalina.*

---

[1] Journ. of Conchology, iii, 1880, p. 95.

The reason for this great development of the buccal mass is to be found in the carnivorous habit of the members of the group. This habit, in whatever class of animals it occurs, is invariably accompanied by an enlargement, either of the prehensile organs, or of the jaw armature (usually the teeth), or of both. In the case under consideration, the buccal mass, with its odontophore, has to serve both as a prehensile and a masticatory organ, and is consequently correspondingly enlarged.

Natalina itself preys on snails, into whose shells it creeps, and then, by the aid of its powerful buccal muscles and large hooked teeth, literally scrapes the inhabitants out mouthful by mouthful. The specimens kept alive by me would clear out the shell of a large *Helix* in a few days, and apparently kept steadily at work until this was accomplished, rarely leaving anything but the kidney behind. The greatest difficulty to be overcome by the cannibal must be the piercing of the muscular foot of the victim, which structure when contracted is extremely hard and compact, but this must nevertheless be penetrated in order to reach the underlying soft tissues; and it seems probable that the enormous muscular development of the buccal mass is adapted for this end, since in the allied form *Testacella* we find a very different modification of the muscles of the buccal mass in connection with its different habit, viz. that of seizing and holding the soft body of a worm, while its juices were being sucked out by the muscular œsophagus of the slug.

Musculature of the buccal mass.—Externally we find a thin layer of longitudinal muscular fibres, which attains its greatest development on the ventral side (Pl. XVII, Figs. 4, 5, 7 *e.l.m.*), the contractions of this ventral muscle often causing a flexure on that side of the free end of the buccal mass.[1]

Beneath this is the great constrictor muscle, the fibres of which are arranged transversely. This muscle is broken up into two well-marked portions, especially posteriorly, viz. a small dorsal band (*d.c.*, Fig. 5) and a more extensive and thicker ventral portion (*v c.*, Figs. 5 and 7); the former is attached in places to the odontophoral cartilage.

The remaining muscles are modifications of an original simple longitudinal band, now broken up by the intervention of the odontophoral cartilage into an antero-ventral and a postero-dorsal series, the latter having the greater development.

The antero-ventral muscle supplies the motive force, which pulls the radula forwards over the cartilage and erects the teeth; this muscle attains but slight development in *Natalina* (*v.l.*, Figs. 5 and 7). It is attached in front to the subradular membrane and behind to the odontophoral cartilage; externally it is continuous with a series of tendonous muscles which are attached to the sides of the functional portion of the radula (Fig. 7), and which appear to be concerned in flattening out that structure and separating the teeth.

---

[1] A similar condition is figured by Godwin-Austen for a contracted specimen of *Paryphanta*: Proc. Malac. Soc., Vol. I, 1893, p. 5.

The postero-dorsal longitudinal muscle is enormously developed (*d.l.*, Fig. 5), and is broken up into a large series of distinct muscles arising from all parts of the radula and radula-sac above and behind the odontophoral cartilage. These muscles run obliquely backwards, and are inserted upon the edges and inner surface of the odontophoral cartilage. Posteriorly we find a more compact portion of this muscle, which arises from the under side of the radula and runs back to the extreme posterior end of the odontophoral cartilage. These muscles are the ones upon which the greatest amount of work falls, *i.e.* the pulling in of the radula after the teeth have been inserted in the flesh of the victim, the whole rasping action of the radula depending on the size of the teeth and the power of these retractor muscles.

The odontophoral cartilage has lost all its cartilaginous nature, its muscular elements alone remaining; it is here a long scoop-shaped mass of muscular tissue, whose fibres are extremely short and arranged vertically to the surface of the scoop. Besides giving support to the radula and attachment to its muscles, it is itself an important motor of that structure, the contraction of its fibres acting in the same way as the intrinsic muscles of the human tongue, and producing an elongation of this structure and a consequent protrusion of the radula.

A mass of longitudinal muscular fibres is attached to the free edge of the odontophoral cartilage on either side near the anterior end; this mass probably bends up the free end of the scoop, and so assists the rasping action of the radula (*l.o.m.*, Fig. 6): it is, like the preceding, an intrinsic muscle. The extrinsic muscle of the cartilage consists of a series of adjustor muscles (Figs. 6 and 7 *o.a.*).

The radula has been fully described by Pilsbry. The radula-sac is very long, running through the buccal mass in the dorsal groove of the odontophoral cartilage, close to which it lies anteriorly, but posteriorly it becomes buried up in the great retractor muscle of the radula, eventually appearing on the dorsal surface of the buccal mass near its posterior end, which, however, it does not quite reach.

The retractors (*r.m.*, Fig. 4) of the buccal mass are attached to the sides and dorsum of that structure near its posterior end, and pass into the great columella muscle. A numerous series of protractors, etc., pass from its anterior end to the cephalic wall round the mouth (Fig. 4).

The combined action of these muscles may be explained in the following manner:—The odontophore would be protruded by the contraction of the transverse vertical fibres of the odontophoral cartilage, assisted by the great sphincter muscles of the buccal mass; these latter would further serve to press the tongue firmly against the flesh of the prey; a contraction of the antero-ventral longitudinal muscles would then pull the radula forward, the convex smooth anterior surface of the teeth gliding over the food till the teeth were fully erected; this would be followed by a contraction of the levator muscles of the front of the odontophore, both intrinsic and extrinsic, thus lifting up the scoop and driving the teeth into the flesh, accompanied almost simultaneously by a contraction of the great postero-dorsal longitudinal

muscle, which pulls the radula with its erected teeth back over the surface of the cartilage into the mouth, and tears the teeth through the flesh of the victim, thus rasping away a portion of it, and carrying the spoil into the buccal cavity, from which it would pass into the œsophagus.

A comparison of the buccal mass of *Natalina* with that of *Testacella* shows certain interesting modifications, obviously due to the different methods of feeding in the two animals. First, we notice the almost entire reduction in the latter of the great constrictor muscles of the buccal mass, the outer sheath of that structure being very thin and containing but few longitudinal and transverse muscular fibres. The various internal longitudinal muscles are well developed, the antero-ventral series and the lateral muscles (Figs. 8 and 9) being larger than in *Natalina*; the postero-dorsal series is peculiar in the fact that its component muscles perforate the wall of the buccal mass, and are attached to the left body-wall of the slug instead of to the odontophoral cartilage.

The radula-sac of *Testacella* is very short, and hardly extends behind the anterior half of the buccal mass; on the other hand, the functional radula extends below the cartilage for a considerable distance backwards, when at rest even further back than the radula-sac does above (Fig. 8).

The buccal cavity is much larger, and the odontophore and buccal mass are capable of much greater evagination than in *Natalina*.

Testacella feeds on worms, which it must seize by a very rapid protrusion of the tongue; to facilitate this the buccal cavity can be everted, the tongue pushed forwards by the contraction of the intrinsic muscles of the odontophoral cartilage, and the teeth, which are like barbed needles rather than curved hooks, are shot into the prey; then all the longitudinal muscles come into play and pull a considerable part of the worm thus hooked into the large buccal cavity and hold it there while its blood is sucked out. This slug does not normally use its radula as a rasping organ after the manner of *Natalina*, consequently it does not need any great constrictor muscles for pressing the tongue against the body of its prey, but owing to the more active nature of its victim it needs a more rapidly acting and prehensile tongue.

The œsophagus of *Natalina* opens dorsally into the buccal cavity near the anterior end of the buccal mass, and just over the odontophore the two salivary glands open into it. These glands are a pair of long compact masses (*s.g.*, Figs. 1 and 2) situated at the sides and meeting above the œsophagus, but remaining quite distinct from one another.

The condition of the salivary glands is rather variable amongst the Agnatha, *N. Trimeni*[1] possessing only the right gland and duct,

[1] I should be inclined to regard the specimen of *N. Trimeni* described by Pace as abnormal in this respect, for in most Mollusca where the salivary gland is a single mass, that structure owes its origin to a fusion of two distinct glands, always, however, retaining their two ducts, as in *Paryphanta* (*fide* Godwin-Austen, Proc. Malac. Soc., I, 1893, p. 5).

Paryphanta a median gland with two ducts, while the other forms, as far as is known, possess two distinct glands and ducts.

The œsophagus in both specimens which I have examined was a contracted thick-walled tube. It is probably highly distensible.

Pace, in describing the anatomy of *N. Trimeni*, speaks of the œsophagus being displaced to the right side of the buccal mass owing to the enlargement of the latter; now in both my specimens, if it were displaced at all, it was to the left, and this displacement appears to be due rather to the enlarged hermaphrodite duct than to the buccal mass, unless one regards the latter as causing a displacement of the former, which consequently pushes the œsophagus to the left.

The rest of the alimentary canal (Fig. 1) calls for no special comment, and closely resembles that of *Helix*.

The pulmonary chamber is large, and its outer wall highly vascular (Fig. 1), the heart in its pericardium being situated in the left posterior corner of this chamber; a large kidney is on the right of the pericardium and opens by a short ureter (*u.*) into the pulmonary chamber close to its posterior limit, there being no long recurved ureter as in *Helix*.

The arterial system was injected in a fresh specimen, but showed no marked differences from that of *Helix*; only, the buccal mass being very large, it consequently receives much larger branches than the corresponding organ in the common snail.

The pedal gland, as noted by all, attains enormous development in the Agnatha, and especially in *Natalina*, where it is generally doubled once or twice on itself. In *N. Caffra* it opens as usual between the head and foot, just below the mouth, and then extends back in the body cavity as a thick-walled, slightly convoluted tube situated immediately below the great retractor muscle, the course of which it follows for a short distance towards the visceral dome, when it suddenly bends sharply on itself and runs forwards and downwards, only to bend back again into the substance of the foot, where it ends blindly.

Reproductive organs.—The genitalia of *Natalina* have been described by Pilsbry and Pace from imperfect specimens. In both examples of *N. Caffra* which I have examined the genital organs were enormously developed, especially the albumen gland and the hermaphrodite duct. The ovotestis is situated in the right lobe of the liver, and consists of numerous cæcal tubes communicating with a closely coiled duct (*h.d.*, Fig. 1); this enters a huge albumen gland divided into a glandular and a coiled portion, the commencement of the hermaphrodite duct, which becomes a large, much convoluted tube divided into a well-marked opaque, brownish, prostatic portion (*pr.*) and a translucent, white, oviducal duct (*ov.*). The former communicates with a slightly coiled vas deferens (*v.d.*), which opens into the end of the penis sac (*p.*); this sac is bent on itself, the retractor muscle (*r.p.*) being attached at the angle. The portion between the vas deferens and the angle, contains the protrusible penis: the remaining portion communicates with the genital cloaca. After giving off the vas deferens the rest of the hermaphrodite duct passes